INHERITANCE OF RESISTANCE TO LEAF RUST IN THE CROSSES WICHITA X MEDITERRANEAN, WICHITA X MALAKOF, WICHITA X HUSSAR, AND PAWNEE X MEDITERRANEAN

by

ROBERT LEWIS SCHULTE

B. S., Kansas State College
of Agriculture and Applied Science, 1952

A THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Agronomy

KANSAS STATE COLLEGE
OF AGRICULTURE AND APPLIED SCIENCE

1957

TABLE OF CONTENTS

INTRODUCTION

Leaf rust of wheat, Puccinia triticiana, Erikss., an obligate parasite, is one of the most destructive wheat diseases. One-hundred and sixty-three physiologic races are recognized (9). These races are differentiated on the varieties Malakof, Democrat, Mediterranean, Hussar, Loros, Brevit, Carina, and Webster. As resistant varieties offer the best means of control, studies are in progress at Kansas State College to determine the genetic factors present in these differential varieties and the manner of transferring these factors into the Kansas accepted hard red winter wheat varieties, Pawnee and Wichita. This thesis is a part of that study.

REVIEW OF LITERATURE

Chester (1) reviewed the history, life cycle, economic importance, symptoms, cause, and physiologic specialization of leaf rust as well as the environmental factors affecting its survival and development. In addition he presented the studies of inheritance of resistance published prior to 1940. The majority of these studies indicated that leaf rust resistance was inherited in a simple Mendelian manner -- the genes being completely dominant, incompletely dominant, or recessive depending upon the race or race groups used in the tests. A single factor often controlled resistance to several races. Chester stated that Shekhurdin in 1926, and Wismer in 1934, found transgressive segregation for leaf rust resistance in crosses of two susceptible varieties,

indicating that recessive factors were responsible for resistance and that inheritance could be explained as being due to multiple factors.

The reaction of the differential varieties, Pawnee, and Wichita to eight physiologic races of leaf rust and the results of inheritance studies at Kansas State College are summarized in Tables 1 and 2 respectively.

Table 1. Reaction of differential varieties, Pawnee, and Wichita to eight races of leaf rust used in inheritance studies at Kansas State College.

Variety and CI Number		Physiologic Race							
		5	9	11	15	19	35	58	126
Malakof	4898	4*	4	0	0	4	4	0	4
Democrat	3778	4	0-1	0-2+	4	0	4	4	4
Mediterranean	3780	4	0-1	1-2	4	0	4	4	4
Hussar	3756	0-2+	1-2+	0-2	0-1	1	1	2	2-
Loros	3384	0-1	4	3-4	0-1	4	4	3	4
Brevit	3779	0-1	1-2	3-4	0-1	2	2+	4-3	2
Carina	3332	0	1-2	2-	0	4	2+	2	1
Webster	4843	0-1	4	1-2+	0	4	4	1	1
Pawnee	11669	4	0-1	0-1	4	0-1	4	4	4
Wichita	11952	4	4	4	4	4	4	4	4

*Reactions taken from the Fifth Revision of the International Register of Physiologic Races of Leaf Rust (8) and records of the Kansas State College cooperative wheat breeding project.

Table 2. Best fitting F_3 segregation ratios of crosses among leaf rust differentials and Pawnee and Wichita wheat.

	Physiologic Races					
	5	9	11	15	19 : 35	58 : 126
Crosses studied by Woodward (1950)						
Malakof x Democrat		1:8:7		1:2:1		1:2:1
Democrat x Mediterranean		Identical		Identical		Identical
Crosses studied by Mode (1953)						
Webster x Mediterranean	1:2:1	1:2:1		1:2:1		1:2:1
Carina x Hussar	4:4:2:2: 2:1:1	7:8:1		4:4:2:2: 2:1:1		7:8:1
Carina x Pawnee	Linked Duplicate Genes			Linked Duplicate Genes		Linked Duplicate Genes
Brevit x Hussar		7:8:1		7:8:1		
Carina x Malakof	1:2:1				1:2:1	
Loros x Pawnee	1:2:1					
Webster x Pawnee	1:2:1					
Crosses studied by Harris (1955)						
Hussar x Democrat	1:15 (1:8:7)	37:26:1 19:38:7			1:15 (1:8:7)	

Table 2. (concl.)

	Physiologic Races							
	5	9	11	13	14	35	58	126
Mediterranean x Hussar	1:3:7	7:8:1	2:12:2			1:15 (1:3:7)		
Brevit x Mediterranean*	3:1	15:1						1:15
Brevit x Carina*	Identical	7:9						9:7
Webster x Brevit*	Identical	7:9						3:1
Loros x Webster*	Identical	Identical						3:1
		Crosses studied by Shulte						
Wichita x Mediterranean		1:2:1						
Wichita x Malakof				1:2:1				
Wichita x Hussar	1:2:1			1:2:1				
Pawnee x Mediterranean		Identical						

* Cross studied in F_2 generation.

Woodward (10) studied the F_2 progeny of the crosses Malakof x Democrat, and Democrat x Mediterranean to physiologic races 9, 15, and 58. He concluded that two complementary recessive factors carried by Democrat govern resistance to race 9. Malakof had a single factor for resistance to races 15 and 58, which has inherited independently of the factor governing reaction to race 9. Democrat and Mediterranean apparently carried the same factors for reaction to these three races.

Mode (8) studied the reaction of the cross Webster x Mediterranean to races 5, 9, 15, and 58; Carina x Hussar to races 5, 9, and 15; Carina x Pawnee to races 5, 15, and 58; Brevit x Hussar to races 9 and 15; Carina x Malakof to races 5, 15, and 19; and Loros x Pawnee and Webster x Pawnee to race 5. His conclusions are quoted as follows:

> Webster had one dominant factor for resistance to races 5, 15, and 58. Mediterranean had one incompletely dominant factor for resistance to race 9. In the Webster x Mediterranean cross, resistance to race 9 and to races 5, 15, and 58 were inherited independently. The resistant reaction of Webster was also completely dominant and monofactorially inherited in the Webster x Pawnee cross tested to race 5. The behavior of Carina was inconsistent in the three crosses tested, suggesting the variety was composed of different genotypes for rust reaction. Carina and Hussar carried different genes for resistance to races 5, 9, 15, and 58. The Carina reaction to races 5 and 15 was epistatic to the Hussar reaction, when the Carina genes for resistance were homozygous. The reaction to race 9 and to races 5, 15, and 58, which appeared to be due to the same genes, were not independently inherited. Carina and Pawnee were differentiated by linked duplicate genes in coupling with 18.7 ± 2.3 percent crossing over in their reaction to races 5, 15, and 58. The behavior of the Carina x Malakof cross tested to race 5 in which resistance appeared to be conditioned by a single gene could not be adequately explained. Three factors appeared to be involved in the transgressive segregation for susceptibility to race 15 and high resistance to race 19 in the Carina x Malakof cross tested to these races. Brevit and Hussar

carried different genes for resistance to races 9 and 15. The reactions to races 9 and 15 were associated in inheritance to this cross. The resistance of Loros to race 5 was differentiated from the susceptibility of Pawnee by a single gene. The reaction of Loros was incompletely dominant.

Harris (2) studied the reaction of the F_3 progeny of the crosses Hussar x Democrat, and Mediterranean x Hussar to races 5, 9, 11, and 35. In addition he studied the reaction of the F_2 progeny of the crosses Brevit x Mediterranean, Brevit x Carina, Webster x Brevit, and Loros x Webster to race 5. These were grown to maturity and tested to races 9 and 126. Tests with races 5 and 35 gave inconclusive results in the progeny of the crosses involving Hussar which was attributed to environmental factors. Mediterranean, Hussar, and Democrat appeared to have different factors for resistance to races 9 and 11. Mediterranean and Hussar each had a dominant factor for resistance to race 9 and two factors each for resistance to race 11. Democrat had two factors for resistance to race 9 and one factor for resistance to race 11. Factors for resistance in Hussar to races 5, 9, 11, and 35 were associated in the crosses Mediterranean x Hussar and Hussar x Democrat.

Brevit, Carina, Webster, and Loros apparently carried a dominant, identical factor for resistance to race 5. Brevit carried a dominant factor for resistance to race 9, but this was apparently recessive to two complementary dominant factors for susceptibility carried by Carina in the adult stage. Webster and Loros had the same factors for susceptibility to race 9. Carina

had two complementary factors and Webster had one dominant factor for resistance to race 126. Under conditions of the tests in 1954-55, Carina was resistant to race 9 in the seedling stage and susceptible in the adult stage; Brevit was resistant to race 126 in the seedling stage and susceptible in the adult stage.

Heyne and Johnston (7) concluded from a study of crosses involving Pawnee, RedChief, and Timstein, that Pawnee carried one major factor for resistance to race 9 in the seedling stage and that this factor was nonallelic and partially epistatic to the factor governing resistance to race 9 in Timstein.

Heyne and Livers (5) studied crosses of Chinese monosomics x Pawnee and obtained a 9:7 ratio in the F_2, thus indicating resistance due to complementary factors. Since other studies indicated that Pawnee had one major factor for resistance to race 9, the authors suggested alternative conclusions. One was that Chinese may have contributed a susceptibility factor that was partially epistatic to the resistant reaction of Pawnee. The alternative conclusion was that Pawnee carried two complementary factors and that in previous studies which gave simple segregation, the varieties used had one of the factors in common with Pawnee.

METHODS AND MATERIALS

F_3 progeny of the crosses Wichita x Mediterranean, Wichita x Malakof, and Wichita x Hussar, were studied for seedling reaction in the greenhouse during the winter of 1955-56. The Wichita x Mediterranean hybrid was tested to race 9; Wichita x Malakof to

race 15; and Wichita x Hussar to races 5 and 15. The reaction of the F_3 progeny of the cross Pawnee x Mediterranean was studied as part of the cooperative wheat breeding project during the winter of 1954-55, and the analysis of these results are included as a part of this thesis.

The method of innoculation used in this experiment was the same as that used by Woodward (10), Mode (8), and Harris (2). Approximately 25 seeds of each F_2 plant were sown in 3 inch pots. Ten days after planting, the plants were innoculated with a pure culture of a known physiologic race of leaf rust. The plants then were placed in a moist chamber, moistened, and dusted with urediospores from plants which previously had been infected. Only one race was used at a time in the study, and prior to changing races, the greenhouse was washed as a precaution against race mixtures. 100 pots of the F_3 lines, with appropriate parents, and differentials for detecting race mixtures, were studied at one time. Plants were removed from the moist chamber approximately 15 hours after innoculation.

In 8 to 11 days, depending on temperature and light intensity, the plants were classified as to phenotype on the basis of type of uredia formed. The basic reaction types used were described by Mains and Jackson (7) as follows:

0 - Highly resistant - No uredinia formed; small flecks, chlorotic or necrotic areas more or less prevalent.

1 - Very resistant - Uredinia few, small, always in small necrotic spots. More or less necrotic areas produced without development of uredinia.

2 - Moderately resistant - Uredina fairly abundant, of moderate size, always in necrotic or very chlorotic spots. Necrotic spots seldom without uredinia.

3 - Moderately susceptible - Uredinia fairly abundant, of moderate size. No necrosis produced, but sometimes slight chlorosis immediately surrounding the uredinia.

4 - Very susceptible - Uredinia abundant, large. No necrosis or chlorosis immediately surrounding the uredinia. Infected areas sometimes occuring as green islands surrounded in each case by a chlorotic ring.

An intermediate reaction classified as "Y" (3) and characterized by a 4-type uredinia on the upper part (distal end) of the leaf which gradually changed to a 0 (zero)-type at the base (proximal end) was observed in the progeny of the Wichita x Mediterranean cross when tested to race 9.

Plants in each pot, the progeny of an F_2 plant, were classified as resistant, segregating, or susceptible and plants in segregating pots were counted and individually classified as to reaction type.

EXPERIMENTAL RESULTS

Reaction of F_3 Progeny of Wichita x Mediterranean to Race 9

The Wichita parent was characterized by a 4-type reaction. Hybrids classified as susceptible were similar to Wichita in reaction type. The Mediterranean parent generally was classified as having a 0-type reaction, but not all Mediterranean plants gave that response. The results of the reaction of Mediterranean to race 9 are given in Table 3.

Table 3. Reaction of Mediterranean to Puccinia triticina, race 9.

Pot no.	Reaction*	Pot no.	Reaction
1	0-21; Y-2	10	0-28
2	0-7; Y-13; 4-1	11	0-30; Y-1
3	0-28	12	0-28; Y-2
4	0-28	13	0-34; Y-1
5	0-30; Y-4	14	0-24; Y-1; 4-1
6	0-14; Y-1	15	0-32; Y-1
7	0-28	16	0-24; Y-1
8	0-29; Y-1	17	0-28
9	0-28		

* The first letter or number is the reaction type; the second, the number of plants in the pot showing that reaction.

Six of the progeny of the 17 Mediterranean plants studied gave the expected response that all plants were resistant. Nine of the plant progenies had one or more plants with a Y reaction, and two plant progenies had one or more plants with a Y reaction and a 4-type reaction -- one of which (No. 2) was decidedly off-type.

Chester (1) reported that variation in the response of Mediterranean had been observed by other workers. The off-type reaction of Mediterranean may have been due to mixtures, to outcrosses, to mutations for susceptibility, or to the influence of micro-environment. Whatever the cause of these off-type responses to race 9, the rate of occurrence (3.39% omitting plant

No. 2) was exceedingly high for either outcrossing or mutation. Chester (1) reported the work of many investigators who had determined that the leaf rust reaction of several wheat varieties was highly influenced by environmental factors. Investigation of variation in Mediterranean should be carried out.

Information obtained on the F_3 lines of the Wichita x Mediterranean cross is presented in Table 4.

Table 4. Segregation of F_3 lines of Wichita x Mediterranean tested to race 9.

Response	No. of F_3 lines	Hypothesis	Chi-square	P value
Res	73	1	.314	.80<P<.90
Seg	157	2		
Sus	79	1		

There appeared to be a one factor difference in this cross for reaction to race 9, with the response of the Mediterranean factor for resistance being partially dominant. Segregating lines contained plants having 0, 4, and Y-type reactions. The number of plants of each reaction type were totaled and following results were obtained:

Table 5. Manner of segregation in segregating F_3 lines of Wichita x Mediterranean tested to race 9.

Response	No. of plants showing response	Hypothesis	Chi-square	P value
0	987	1	15.220	P<.001
Y	1730	2		
4	980	1		

The hypothesis of a single partially dominant factor difference in the Wichita x Mediterranean cross was supported by the data shown in Table 4 for the manner of segregation of the F_3 lines. The Mediterranean factor governing resistance to race 9 appeared to be much more stable in the hybrid than in the parent. Failure to support the hypothesis by individual plant counts in segregating F_3 lines (Table 5) could not be adequately explained. However, only three phenotypes occurred in the F_3 segregating lines. This observation gave further support to the hypothesis of a single factor difference, and precluded the application of other hypotheses.

Reaction of F_3 Progeny of Wichita x Malakof to Race 15

The Wichita parent gave a 4-type reaction and the Malakof parent a 0-type reaction. Only two reaction types appeared in the segregating lines and those were phenotypically similar to the parents. The results of the study of segregation in the F_3 generation of Wichita x Malakof are given in Tables 6 and 7.

Table 6. Segregation of F_3 lines of Wichita x Malakof tested to race 15.

Response	No. of F_3 lines	Hypothesis	Chi-square	P value
Res	89	1	4.456	.10<P<.20
Seg	157	2		
Sus	63	1		

Table 7. Manner of segregation in segregating F_3 lines of Wichita x Malakof tested to race 15.

Response	No. of plants showing response	Hypothesis	Chi-square	P value
0	3683	3	2.054	.10<P<.20
4	1286	1		

The resistance of Malakof appeared to be due to a single gene which was completely dominant to the susceptibility of Wichita. In experiments completed to date, complete dominance for resistance has been found less often than partial dominance in the differential varieties.

Reaction of F_3 Progeny of Wichita x Hussar to Race 5

A 4-type reaction was observed on the Wichita parent. The reaction of Hussar varied from 1- to 2+ with one plant progeny having several plants showing a Y-type reaction. The majority of the parent plants showed the 1-type reaction. The intermediate type was designated as a 2 in this cross. In general the reaction of the hybrid differed from the Hussar reaction in that the pustules were larger and more numerous. The manner of segregation of F_3 lines of Wichita x Hussar to race 5 is presented in Table 8.

Table 8. Segregation of F_3 lines of Wichita x Hussar tested to race 5.

Response	No. of F_3 lines	Hypothesis	Chi-square	P value
Res	78	1	.243	.80<P<.90
Seg	151	2		
Sus	72	1		

There appeared to be a single gene difference between the reaction of Wichita and of Hussar to race 5. However, this hypothesis was not supported by the segregation ratio of the segregating lines. A 1:1:1 ratio was obtained and that did not correspond to a known genetic ratio.

These results may be explained by the difficulty encountered in classifying the intermediate type in that cross. Reference is made to the fact that the progeny of Hussar was observed as having a range of reaction types from 1- to 2+, and that it included plants that showed the 2-type reaction which was considered as the intermediate type in segregating lines.

Mains and Jackson (7) noted that Hussar was quite variable in its reaction to some of the physiologic races. It was often highly resistant in late fall and winter and only moderately or slightly resistant in the spring. Chester (1) reported that Dodov (1931a), Roberts (1936) Waterhouse (1929-30), Hassebrauk (1937), and Newton and Johnson (1941) found that some of the differential varieties gave different reaction types under different light intensities.

The experiments of Newton and Johnson (1941), as reviewed by Chester (1), were the most closely controlled. Newton and Johnson maintained a constant temperature and observed changes of reaction of seven wheat varieties to seven races of leaf rust under the changing light conditions from February to April. In many cases a complete change from resistance to susceptibility was observed.

According to Chester (1) various workers have found that soil

fertility, temperature, and humidity also affect reaction type. In general, factors which increase the vegetative growth of the wheat plant such as increased percentage of nitrogen, increased temperature, or increased humidity, also tend to increase the susceptibility of wheat to leaf rust.

Certain members of the differential varieties are more stable under environmental changes than others. Chester (1) reported that Newton and Johnson rated the differentials according to the degree their reaction types were affected by environment as follows: 0 percent for Loros, 13 percent for Malakof, Mediterranean, and Democrat, 40 percent for Webster, 53 percent for Carina and Brevit, and 67 percent for Hussar.

The sensitivity of the reaction type of Hussar to changes in environment may account for the difficulty encountered in classifying plants in the segregating lines, as each plant was actually in a separate micro-environment.

Since genetic studies reported in this thesis were not conducted under controlled environment, it was not possible to clearly distinguish the effects of environment from the effect of heredity in the Wichita x Hussar cross when tested to race 5.

Reaction of F_3 Progeny of Wichita x Hussar Tested to Race 15

The Wichita parent gave a 4-type reaction. The Hussar parent reaction type varied from 1- to 2+, but the majority of the plants showed the 1- type response. Reaction types 2 and Y were observed as the intermediate types in this cross. The manner of segregation in the hybrid lines is presented in Table 9.

Table 9. Segregation of F_3 lines of Wichita x Hussar tested to race 15.

Response	No. of F_3 lines	Hypothesis	Chi-square	P value
Res	78	1	.660	.70<P<.80
Seg	153	2		
Sus	69	1		

There appeared to be a single partially dominant factor for resistance carried by Hussar. As in the case of reaction to race 5, the data of segregation in segregating lines did not give a basis for a logical explanation of the factors controlling resistance in this cross. The results were attributed to the variable response of Hussar under fluctuating environment.

Association of Factors for Resistance to Race 5 and Race 15 in the Cross Wichita x Hussar

The association of reaction to physiologic races 5 and 15 in the cross Wichita x Hussar is given in Table 10.

Table 10. Association of reaction of F_3 lines of the cross Wichita x Hussar to physiologic races 5 and 15.

Reaction to race 5	Reaction to race 15			
	Resistant	Segregating	Susceptible	Total
Resistant	76	2	0	78
Segregating	3	148	0	151
Susceptible	0	3	69	72
Total	79	153	69	301

Chi-square = 554.9 d.f. = 4 P<.001

The same factor in Hussar apparently controlled the resistance to both race 5 and 15 in the cross Wichita x Hussar. Of 301 lines, 293 gave the same reaction to both races. In no case was the reaction completely reversed, i.e., if a line was resistant to race 15, it did not give a susceptible reaction to race 5 or vice versa. The lack of perfect agreement was due to three F_3 lines that were classified as resistant to race 15 and segregating to race 5, to two F_3 lines that were classified as resistant to race 5 and segregating to race 15, and to three F_3 lines that were classified as susceptible to race 5 and segregating to race 15. This result could be attributed to chance alone, since only a small number of progeny (25) were used for each F_3 line.

Reaction of F_3 Progeny of Pawnee x Mediterranean to Race 9

Pawnee and Mediterranean each gave a 0-type reaction to race 9. All of the hybrid lines except one (line No. 14267) were classified as resistant. The off-type line segregated in a 1:2:1 ratio and appeared to be an F_2 of an outcross. Pawnee and Mediterranean appeared to have the same factor for resistance to race 9. However, of the 562 F_3 lines tested, 537 had all 0-type plants and 25 had plants which varied in reaction type from 1 to 4. Response of the off-type lines is given in Table 11.

The intermediate type reactions ranged from 1 to 2++, and included the Y-type. Those reactions may have been due to a common factor which was inherent in the germplasm of Mediterranean. These reaction types are so similar that a different person

Table 11. Response of off-type F_3 lines of Pawnee x Mediterranean tested to race 9.

1954 Line Number	Total* Plants	No. of Plants Showing Off-type Response							
		2+	2++	2	2-	Y	1	4
13752	25	1						
13788	25		2					
13809	25	1						
13841	25			1				
13960	25			1				
13999	25				1			
14012	25							1
14018	25							1
14022	25							1
14029	25							1
14045	25					2		
14052	25			1				
14056	25	1						1
14060	25	1						
14067	25	1						
14070	25							1
14085	25					1		
14138	25							1
14174	25							
14182	25			1				
14238	25					2		
14247	25					2		
14267**	19					9		5
14271	25					6		
14351	25						1	
Total	619	5	2	4	1	22	1	12

* The total number of plants is estimated as 25 plants per line.
** An actual plant count was taken of line number 14267.

may have classified the reactions in a manner different from that shown in Table 11. A less exacting person even may have classified them all under one type. Chester (1) noted that such intermediate reaction types tend to be unstable toward environment. It is possible that the variability in reaction type indicated in Table 11 may have been due to micro-environment.

Omitting line 14267, and basing an estimate of the population on 25 plants per line studied, the variable types were calculated to comprise .24 percent of the population. This small percentage could be attributed to mixtures, to outcrossing or to environmental variation. Due to the variable response of Mediterranean, further investigation of this cross should be conducted.

DISCUSSION

Heyne and Johnston (4) stated that studies at Kansas State College concerning the development of agronomically desirable wheat varieties resistant to leaf rust, consists of three interrelated phases. The first is an inheritance study, a part of which has been presented in this thesis. This study has as its aims, the determination of the number of genes controlling reaction to each of the physiologic races and the allelic relationships between genes.

The second phase is a monosomic analysis to supplement the inheritance studies, particularly in regard to linkage relationships. Attempts are being made to develop monosomics for each of the 21 chromosomes of Pawnee and Wichita. Whole

chromosomes carrying resistance can then be transferred from the differential varieties to Wichita and Pawnee. A direct monosomic analysis of the eight differential varieties is also being carried out using the Chinese monosomics as the tester parents.

The third phase is a backcross program which involves the differential varieties and Wichita. The variability of reaction types of the differentials due to environment has been discussed previously in conjunction with the F_3 progeny reaction of the cross Wichita x Hussar. One objective of the backcross program is to develop a set of differential wheat varieties so that the factors for resistance are in a common genetic background.

Pawnee wheat has been found to carry factors which modify the reaction types of progeny of crosses of Pawnee and the differential varieties. Its use therefore has been discontinued. Studies to date have shown Wichita to consititute a stable genetic background in regard to leaf rust reaction. This will be confirmed only when studies of all combinations of Wichita and the differential varieties have been completed.

Another objective of the backcross program is to combine different sources of resistance to the same physiologic race into the variety Wichita. For example, suppose that the 0-2 type reaction of Hussar, the 0-1 reaction of Loros, Brevit, and Webster, and the 0-type reaction of Carina to race 5 are found to be controlled by five independent non-allelic factors. These factors could be combined in the genetically stable variety Wichita by backcross procedure. If, however, the 0-1 type reaction of Loros, Brevit and Webster is allelic to the 0-type reaction of Carina

these two types of resistance can not be combined, since only one phenotype of a given character can express itself in any one plant. The combination of all possible factors for resistance to a given race should act as an extensive protection against mutation in the wheat plant or to the occurrence of new biotypes of a race or even to the occurrence of new races. If Wichita possessed different factors for resistance to a given race and one of the factors mutated to the susceptible form, the reaction of "resistant Wichita" might not change to susceptibility because the other genes would continue to give resistance. Should a mutation occur in the parasite and only one factor for resistance be present in the host, the reaction might change from resistance to susceptibility. But if a number of factors for resistance were present in the host, there would be greater chance that one or more of the factors would control resistance to the mutant race of rust.

Studies reported in this thesis have shown that the 0-type resistance of Malakof to race 15, the 0-2+ type resistance of Hussar to races 5 and 15, and the 0-1 type resistance of Mediterranean to race 9, can all be added to Wichita.

Analysis of crosses to determine the manner of combining resistance to various races may proceed in the following manner. Democrat and Mediterranean show a resistant reaction to race 9 and a susceptible reaction to races 5, 15, and 58. Woodward's study (10) indicated that Mediterranean and Democrat carry the same factors for resistance and susceptibility to these four races. Webster is resistant to races 5 and 58, and susceptible to race 9.

Mode (8) found in his study of the Webster x Mediterranean cross that the reaction to race 9 and the reactions to races 5, 15, and 58 were inherited independently. Thus, the resistance of Democrat and Mediterranean to race 9 could be combined with the resistance of Webster to races 5, 15, and 58.

Mode (8) found that the resistance of Webster to races 5, 15, and 58 was due to the same gene. Webster and Brevit show a 0-1 type reaction to race 5; however, Brevit exhibits a 1-2 type reaction and Webster a 4-type reaction to race 9. Harris (2) showed that Webster and Brevit carry an identical factor for resistance to race 5, and complementary factors for resistance to race 9. Thus the resistance of races 5, 15, 58, and 9 also could be combined in Wichita by means of a backcross program involving Wichita, Brevit, and Webster.

When all of the possible crosses among the differentials have been studied, a sound basis for building a rust resistant Wichita wheat, and a set of stable leaf rust differentials will be possible. Meanwhile sufficient information has been obtained to begin the backcross program.

The number of physiologic races is so great that to obtain resistance to leaf rust would appear at the outset to be an impossibility. Chester (1) stated that from the standpoint of practical breeding, it is not necessary to obtain resistance to all races because not all races are present in a given area. This reasoning should be used with caution. A resistant variety, when grown on a large scale, decreases the occurrence of races to which

it is resistant. At the same time races to which the variety is susceptible become more prevalent. Prior to the release of Pawnee wheat, physiologic race 9, to which Pawnee is resistant, was the race that most frequently occurred in the great plains. In recent years due to the extensive production of Pawnee, race 9 has become less prevalent and races 5, 15, 58 and 126, to which Pawnee is susceptible have become more prevalent. Huffman and Johnston (6) stated that 44 races of rust were found in Kansas during the period 1940-1951. Eight of these races were isolated only once. Races that occurred most frequently were 2, 5, 6, 9, 15, 15, 19, 20, 21, 28, 31, 44, 52, 58, 64, 105, and 126.

Chester (1) introduced the concept of resistance to race groups. According to this concept, some of the races classified separately in the "International Register of Physiologic Races" may actually be the same race----the differences in reaction being due only to differences in environment. Chester (1) stated that a pure culture of race 5 gives a race 5 reaction on the differential varieties in February and a race 52 reaction in April. From his observations and from the literature, he grouped as single races those groups of races the reactions of which duplicated those of others of the same group under certain environmental conditions. Thus he considered races 9, 10, 13, 19, 20, 24, 27, 31, 108, and 115 as belonging to the same group and races 2, 3, 15, 25, 34, and 62 as belonging to the same group but different from the first group. In this manner he proposed that only 44 races or groups of biotypes existed at the time his book was published.

There is some genetic evidence that supports the group concept. Chester (1) stated that Dodov (1931a) tested the reaction of 192 wheat varieties to physiologic races 13, 19, 20, and 24 which belong to race group 9, and races 15, 17, and 21 which fall in race groups different from each other and from race group 9. It was found that a given wheat variety exhibited the same reaction to races 13, 19, 20, and 24 and that the reaction to races 15, 17, and 21 bore no relationship to one another or to race group 9.

Heyne and Johnston (4) found that the same factor in Pawnee wheat governs resistance to races 9, 10, 11, 13, 19, 20, 31, and 93.

If the concept of race groups proves valid, breeding for leaf rust resistance will be simplified.

SUMMARY

The inheritance of reaction to several races of leaf rust was studied in the F_3 progeny of the crosses Wichita x Mediterranean, Wichita x Malakof, Wichita x Hussar, and Pawnee x Mediterranean. Leaf rust races 5, 9, and 15 were used in the studies.

Mediterranean appeared to have one partially dominant factor for resistance to race 9 in the cross Wichita x Mediterranean. Makakof had a single dominant factor for resistance to race 15 in the cross Wichita x Malakof. Hussar had a single partially dominant factor for resistance to both race 5 and 15 in the cross Wichita x Hussar. Mediterranean and Pawnee appeared to have the same factor or factors for resistance to race 9.

Variation in response of certain plants of Mediterranean was observed when the variety was tested to race 9, but the cause for these off-type plants was not studied.

ACKNOWLEDGMENT

The author wishes to express his appreciation to Dr. F. G. Heyne, under whose guidance these studies were conducted, for supplying the F_3 lines used in the study, for supplying the data of the Pawnee x Mediterranean cross, for aiding in the preparation of this manuscript, and for his helpful advice during the experiment.

Appreciation is also expressed to Mr. C. O. Johnston for supplying the pure cultures of leaf rust used in the studies and for his help and suggestions throughout the experiment.

LITERATURE CITED

(1) Chester, K. Starr
The cereal rusts. Waltham, Mass: Chronica Botanica, 1946.

(2) Harris, Wallace Wayne
The inheritance of resistance to leaf rust among certain differential crosses of wheat. Unpublished master's thesis. Kansas State College Library. 1955.

(3) Heyne, E. G., and C. O. Johnston
Inheritance of leaf rust reaction and other characters in crosses among Timstein, Pawnee, and RedChief wheats. Agron. Jour. 46: 81-85. Feb., 1954.

(4) Heyne, E. G., and C. O. Johnston
Inheritance of leaf rust reaction among the eight differential varieties of wheat. Wheat Information Service. No. 2, Sept. 1955.

(5) Heyne E. G. and R. W. Livers
Monosomic analysis of leaf rust reaction, awnedness, winter injury and seed color in Pawnee wheat. Agron. Jour. 45: 54-58. Feb., 1953.

(6) Huffman, M. D., and C. O. Johnston
Prevalence and distribution of physiologic races of leaf rust of wheat in Kansas. Transactions of the Kansas Academy of Science, Vol. 55, No. 4, 1952. 419-426.

(7) Mains, E. B., and H. S. Jackson
Physiologic specialization in the leaf rust of wheat, Puccinia triticina, Erikss. Phytopathology 16: 89-120. 1926.

(8) Mode, Charles L.
A study of the number of genes for leaf rust reaction differentiating certain wheat varieties. Unpublished master's thesis. Kansas State College Library. 1953.

(9) Johnston, C. O., and M. N. Levine
"Fifth revision of the international register of physiologic races of Puccinia rubigo-vera (DC.) Wint. F. Sp. tritici (Eriks.) Carleton = (P. triticiana Erikss.), The Plant Disease Reporter. USDA Supplement 238, Oct. 15, 1955.

(10) Woodward, Val Waddoupa
The inheritance of leaf rust resistance in two simple wheat crosses. Unpublished master's thesis. Kansas State College Library. 1950.

INHERITANCE OF RESISTANCE TO LEAF RUST IN THE CROSSES WICHITA X MEDITERRANEAN, WICHITA X MALAKOF, WICHITA X HUSSAR, AND PAWNEE X MEDITERRANEAN

by

ROBERT LEWIS SCHULTE

B. S., Kansas State College
of Agriculture and Applied Science, 1952

AN ABSTRACT OF A THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Agronomy

KANSAS STATE COLLEGE
OF AGRICULTURE AND APPLIED SCIENCE

1957

Leaf rust of wheat is one of the most destructive of the wheat diseases. At present the rust is composed of 163 physiologic races which are differentiated on eight wheat varieties. Host resistance is the best means of controlling the disease, and since the eight differential varieties theoretically carry the germplasm necessary for complete resistance, studies are being conducted at Kansas State College to determine the manner of inheritance of resistance in the differential varieties and the manner of incorporating resistance into agronomically desirable wheat varieties. A portion of that study is described in this abstract.

Previous studies have shown that resistance is usually controlled by one or two factors which are inherited in a simple Mendelian manner.

In this experiment, inheritance of resistance to race 9 was studied in the F_3 progeny of the crosses Wichita x Mediterranean and Pawnee x Mediterranean. Inheritance of resistance to race 15 was studied in the F_3 progeny of the crosses Wichita x Malakof and Wichita x Hussar. The F_3 progeny of the cross Wichita x Hussar were also used in the study of the inheritance of resistance to race 5.

Plants were innoculated approximately ten days after planting by wetting them thoroughly, dusting them with urediospores of the pure culture of the race to be used in the study, and placing them in a moist chamber for approximately 15 hours. Plant response was determined approximately ten days after innoculation, at which

time uredinia were well developed. Only one race at a time was used in the study, and the greenhouse was thoroughly washed prior to changing races to prevent contamination in successive studies.

The scale of resistance proposed by Mains and Jackson, in which the most resistant response was designated by a 0 (zero) and the most susceptible response designated by a 4, was used as the phenotypic classification of the hybrids.

Wichita wheat gave a 4-type response to all races used in the study. The differential variety Mediterranean generally gave a 0-type response to race 9, but some plants exhibited an intermediate type response. The cause of the off-type Mediterranean plants was not determined, and future studies of that variation should be conducted. Resistance to race 9 in the Wichita x Mediterranean cross was found to be controlled by one partially dominant factor carried by Mediterranean.

Pawnee and Mediterranean both gave the 0-type response to race 9, and 561 of the 562 F_3 lines of the Pawnee x Mediterranean cross were classified as resistant. It appeared that the same factor in Pawnee and Mediterranean controlled resistance to race 9.

Malakof gave a 0-type response to race 15. A completely dominant factor carried by Malakof apparently controlled resistance to race 15 in the Wichita x Malakof cross.

The response of Hussar varied from 1- to 2+ to race 5, and from 1 to 2+ in race 15. Segregation of the F_3 progeny of the cross Wichita x Hussar indicated that one partially dominant

factor carried by Hussar controlled resistance to each race. The manner of segregation to race 5 and to race 15 was highly associated, and it was concluded that the same factor or factors in Hussar controlled resistance to both races in the Wichita x Hussar hybrids.

The hypothesis of a single factor difference in the Wichita x Hussar cross tested to races 5 and 15 was not supported by the manner of segregation in the segregating F_3 lines. Failure to support the hypothesis in the segregating lines was attributed to the extreme variation in the response of Hussar under changing environmental conditions.

Further study is necessary for a complete analysis of inheritance of resistance in the differential varieties, but sufficient information has been obtained to proceed with a backcross program to incorporate resistance to several leaf rust races into the variety Wichita.